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VARIATION IN ÆSTIVATION.

BY PROF. W. J. BEAL.

THE great variety of ways in which the sepals and petals of each species meet or overlap each other in the bud is often quite wonderful. In some cases, after examining many flowers, this is found to be true, even in certain species which have been described by some of our best authors as having the parts constantly arranged in a certain definite manner. Take, for example, the diagrams found in Hooker's Le Maout and Decaisne. It would seem as though the artist or the writers of the text, or both, had the idea that sepals and petals were arranged only in a few certain ways, as valvate, convolute, and imbricate in three modes, namely, spiral, opposite in twos, and quincuncial. It would appear by their diagrams that they had been remarkably successful in finding no other forms, or that they had kept throwing away all others as accidental or spurious until those only were found and used which corresponded to their ideal. These remarks will apply with equal force to several other botanical works.

In our best authors on botany, the diagrams showing the æstivation of the sepals of Cruciferæ all appear to be made as they look after the end of the flower-bud is cut off. This shows the sepal next to the axis and the one opposite to it overlapping each edge of the two lateral sepals. There is nothing in such a diagram to indicate that the tip of the anterior sepal overlaps the tip of the posterior. This is the case in all the buds of the several species which I have examined. In the diagrams of all works accessible to me, there is nothing to show that the tip of one of the side sepals overlaps the tip of the other. This overlapping of one lateral sepal was found in all cases examined where the tips were large enough for such purpose. Of fifteen buds of black mustard (*Brassica nigra*) examined, the sepals of

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ten, at their tips, showed the left lateral sepal overlapping the right; in the other five the right lateral sepal was outside the left one. In speaking of the right and left sepals of these flowers, I refer to them as they appear when holding the flower before us with the axis of inflorescence away from or beyond the flower. In the hedge-mustard (*Sisymbrium officinale*) the lateral sepals barely meet, making it impossible to tell which would overlap if they were longer. Of ten buds of *Nasturtium palustre*, seven had the right lateral sepal covering the left; and in three, the reverse was true. The æstivation of the petals of the three preceding species was not easy to determine with certainty, as the tips overlapped but very slightly or not at all.

In Chinese mustard, the æstivation of the sepals was variable, much the same as in the other species above noticed. Fifty flowers were carefully examined. I observed the position of each petal with reference to each other petal, and also its position with reference to the axis. Each of the four petals, or a corresponding petal in different flowers, was found outside; each was found inside. Bearing in mind, as I think we ought, the position of each petal with reference to the axis, I found that the petals of fifty flowers were placed in twelve different ways. In the first twelve examined, the petals were arranged in eight different ways, as follows. The dot indicates the position of the axis: —

Fig. 33.

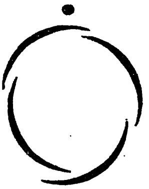


Fig. 34.

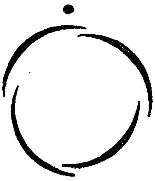


Fig. 35.

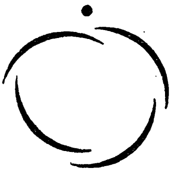


Fig. 36.

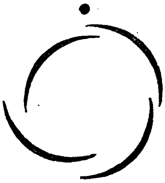


Fig. 37.

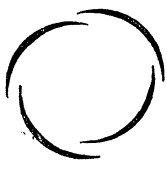


Fig. 38.

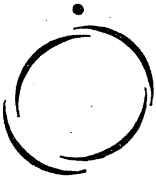


Fig. 39.

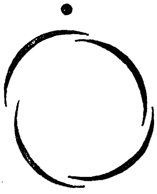


Fig. 40.

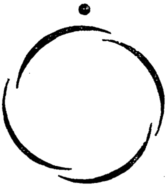


Fig. 41.

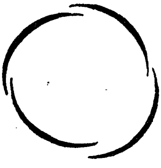


Fig. 42

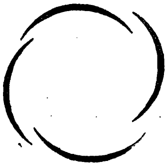


Fig. 43.

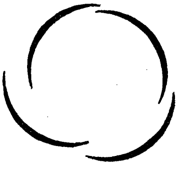
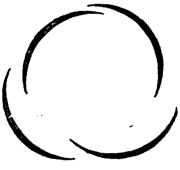


Fig. 44.



Thirteen were represented by Figure 33, six by Figure 34, five by Figure 35, four by Figure 36, three by Figure 37, three by Figure 38, three by Figure 39, three by Figure 40, three by Figure 41, two by Figure 42, two by Figure 43, two by Figure 44, and one by Figure 45.

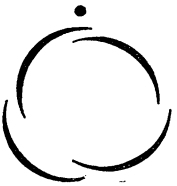


Fig. 45.

With reference to the Cruciferæ, we find in volume i. of Gray's Genera of North America this sentence: "In æstivation, the petals are imbricated with usually one exterior, two half exterior and half interior, and the fourth wholly interior, or else they are regularly convolute." Le Maout and Decaisne say, "Petals variously imbricate in bud." Bentham and Hooker's Genera Plantarum says, "Petals convolute or imbricated with one exterior and the fourth interior." Neither of the above quotations expresses the arrangement for the order. The first comes the nearest because it is the most general of all.

Instead of twelve modes of arrangement for the petals of the fifty flowers mentioned, no doubt the variations would be considerably increased if the position of each petal were observed in its relation to each sepal.

Cleome integrifolia has four small sepals early open in the bud, variously imbricated. The four petals of one hundred flowers were arranged as follows: —

Fig. 46.

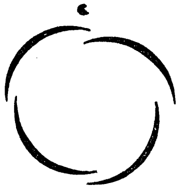


Fig. 47.

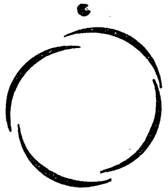


Fig. 48.

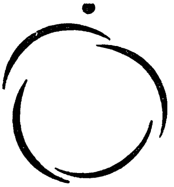
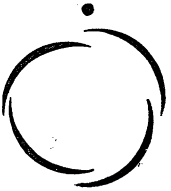
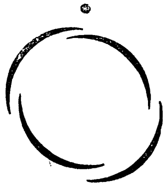


Fig. 49.



Two species of Rosaceæ belonging to two different tribes were examined, namely, *Spiræa urticifolia* and *Agrimonia Eupatoria.* The Spiræa noticed has valvate sepals. The pedicels are too long to make it easy to discover which sepal is next to the axis. The tips of the petals overlap each other in the bud, making it quite easy to determine their relative position. Thirty-three buds were examined, showing fifteen different combinations or sorts of æstivation for the petals, without taking into consideration the position of each with reference to the axis. None were valvate nor regularly convolute, yet, I doubt not, they may be found.

Fig. 50.



Calling the outer petal number one, the next outside number two, and so on, I can show their position as follows by numbers which are here shown as we come to them passing around the flower to the right: —

In 2	flowers the petals formed a spiral to the right	1, 2, 3, 4, 5.
In 2	“ “ “ “ “ left	1, 5, 4, 3, 2.
In 5	“ “ stood thus	1, 4, 5, 3, 2.
In 4	“ “ were quincuncial to right	1, 4, 2, 5, 3.
In 3	“ “ “ “ left	1, 3, 5, 2, 4.
In 3	“ “ “	1, 2, 4, 5, 3.
In 3	“ “ “	1, 3, 5, 4, 2.
In 2	“ “ “	1, 5, 4, 2, 3.
In 2	“ “ “	1, 3, 2, 5, 4.
In 1	flower “ “	1, 2, 5, 4, 3.
In 1	“ “ “	1, 4, 3, 5, 2.
In 1	“ “ “	1, 2, 3, 5, 4.
In 1	“ “ “	1, 3, 4, 5, 2.
In 1	“ “ “	1, 5, 4, 3, 2.
In 1	“ the four petals were	1, 4, 3, 2.
In 1	“ “ “ “	1, 3, 4, 2.

In *Agrimonia* it was very easy to determine the relative position of each sepal and petal, and also the same with reference to the axis. Taking all these things into consideration, of sixteen buds examined closely only two were alike. Undoubtedly there were still many other variations. The five sepals in each case were quincuncial; in eight the spiral went to the right; in eight the spiral went to the left. In all cases observed the second sepal was next to the axis. Of the petals two were arranged in quincunx: with one of these the spiral turned to the right; with the other to the left. The petals of one were convolute; one spirally imbricated to the right, thus, 1, 2, 3, 4, 5. The rest were imbricated in various other ways.

Dr. Gray, Bentham and Hooker, and others speak of the petals of the *Onagraceæ* as convolute (contorta) in the bud. The majority of cultivated fuchsias are not convolute in æstivation.[1]

Of five hundred and seventy-nine buds of *Epilobium angustifolium* the petals of two hundred and eighty-five are convolute, turning to the left, and one hundred and fifty-four to the right. Fifty-three had a single spiral turning to the left, and fifty-three to the right. In twenty-three, two opposite petals covered both edges of the other two. In eight flowers one petal was exterior, one interior, and the other two petals of course were alike half-covered and half-covering. In three flowers one petal was outside and the other three were convolute.

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[1] See note in American Naturalist, page 110, 1876.

Of thirty-eight buds of *Œnothera biennis* thirty were convolute to the right; three buds had one petal outside and the rest spirally turned to the right; two buds had one petal outside and the rest spirally turned to the left; two buds had one petal outside and its opposite one inside; one bud had one petal outside, the numbers running thus, 1, 3, 4, 2, to the right.

Of the order *Asclepiadaceæ* with reference to æstivation Dr. Lindley in Vegetable Kingdom says, " Æstivation of corolla imbricated, very seldom valvular." Dr. Gray in his Manual of Botany, last edition, says, " This order has commonly a valvate corolla which separates it from *Apocynaceæ* which has a convolute corolla." In the *American Journal of Science*, November, 1875, Dr. Gray says, " The type of the latter [*Asclepias*], and the common disposition when the parts are five, is with two pieces exterior, the third exterior by one edge and interior by the other, and two wholly interior." In other words, the petals are quincuncially arranged, the same as alternate leaves on the stem of a cherry-tree. Le Maout and Decaisne say, " Corolla usually contorted." Robert Brown, who gave especial attention to this order, says, " Æstivation of corolla imbricated, rarely valvate."

My first supposition was that I had examined a lot of exceptions to the general rule as stated by such good authority as Gray, especially as it is given as a distinctive mark to separate two related orders. On examining the other authors, I venture to give the results of the number of buds and the name of the species examined.

At the first glance, the corolla of *Asclepias* and *Acerates* seem to be valvate in the bud, but on looking closer, all I have seen are unmistakably convolute.

The petals of	thirty	buds of	*Asclepias*	*incarnata*	were	convolute	to right.
"	five	"	"	*variegata*	"	"	"
"	five	"	"	*tuberosa*	"	"	"
"	five	"	"	*purpurascens*	"	"	"
"	five	"	"	*phytolaccoides*	"	"	"
"	five	"	"	*Cornuti*	"	"	"
"	seven	"	"	*verticillata*	"	"	"
"	five	"	*Acerates*	*viridiflora*	"	"	"

The results, it will be seen, correspond with the account of Le Maout and Decaisne. Probably, Dr. Gray bases his description on other species than those to which I have referred.

In the order *Apocynaceæ*, of forty-three buds of *Apocynum androsæmifolium*, I found the petals all convolute to the right. Five buds of *A. cannabinum* were the same. In nine buds of the former, the sepals were quincuncial to the right, in five buds quincuncial to the left. The other buds of that species were not observed. In the latter (*A. cannabinum*) four buds showed the sepals quincuncial to the left, and one to the right.

It will be observed that the æstivation of *Asclepias* and *Apocynum* are the same, at least so far as the specimens examined are concerned.

In the *Rubiaceæ*, of one hundred and fifty buds of *Cephalanthus* I found that eighteen were convolute, thirteen to the right, three to the left. In Genera Plantarum of Bentham and Hooker, in the tribe containing this species the text says, " Petals never contorted " Keeping in mind the position of all the petals as they stand with reference to each other and to the axis, and noticing the direction of the spirals, I found the petals of thirty-seven buds arranged in twenty-three different modes.

Each of the four petals was found to be outside, each inside, and each occupying either of the intermediate positions.

If we disregard the direction of the spiral and the position of the axis, these twenty-three modes are reduced to six modes.

In the same order, one hundred buds of *Galium asprellum* were all valvate.

Malvaceæ: In four hundred and thirty-three buds of *Malva rotundifolia*, two hundred and one petals were convolute to the right, two hundred and four to the left, fifteen quincuncial, and thirteen as in Figure 31. Lindley and Gray speak of the petals of this genus as convolute.

Fig. 31.

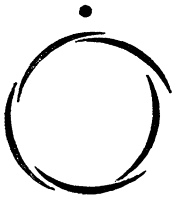
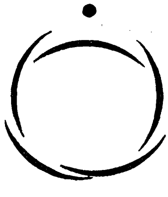


Fig. 32.



Tiliaceæ. In one hundred and seven buds of *Tilia Americana*, fifty-nine were quincuncial, turning to the left, twenty-four to the right, thirteen as in Figure 32; eight had one outside, and then the rest turned spirally to the right. Three were convolute to the left.

Oxalis stricta. Of nineteen buds, ten had the sepals quincuncial to the right, nine to the left. In twelve of these buds the petals were convolute to the right, in five to the left, in one spirally to the right, in one a still different mode.

In *Scrophularia nodosa*, the sepals are imbricated in various modes and some are convolute. In buds of the irregular corolla, the two upper lobes cover the others. In twelve out of nineteen buds, the left lobe of the two outer lobes was outside; in seven the right lobe was outside. It is not easy to determine which is number three and which number four, both covering number five. Of over one hundred flowers of *Phlox Drummondii*, all had the lobes of the corolla convolute to the right. By cultivation and selection for some years, we have numerous permanent varieties or races showing a great variety in color, size, etc., but the æstivation shows no signs of change. I found in one hundred buds of perennial phlox the lobes of the corolla were all convolute to the right. Of over one hundred flower-buds of *Lobelia cardinalis* the lobes of the corolla were all valvate.

From the foregoing examples, I judge that enough attention has not heretofore been given to some of the forms of æstivation which have been thought uncommon. Each sepal and petal should be observed with reference to each other sepal and petal and the axis or bract; also the direction of the whorls or spirals, whether to the right or to the left. The tips of the flower-buds should not be cut off before observing them for diagram or description. Some species are quite constant as to mode, but vary in direction of spirals; others are constant in mode and in direction; others vary as to which sepal or petal is outside the rest. I have introduced no new names to express some of these modes of æstivation, nor have I used all those which others have proposed. In some cases I have preferred to number the outer sepal or petal one, the next within two, and so on till all are numbered. Then begin with number one and place the numbers in a horizontal row as they occur, passing always to the right as the flower is held before the observer. This mode would be of much greater value if we could always tell with ease which sepal or petal was next to the axis or opposite to it. Many authors have copied errors from each other. These errors have, doubtless, many of them been made, authors giving general or definite rules after examining only a few specimens.

As æstivation varies so much where it has been thought so constant, often even in the flowers on the same plant, it seems to me there has been too much stress placed upon certain modes; that it renders of less value the efforts of Jussieu and others to explain or harmonize the quincuncial with other kinds of æstivation. Perhaps we have placed too little stress upon some trivial circumstance or accident in deciding the mode of æstivation in any particular flower.